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TORREYA

Vol. 19 No. 1

January, 1919

THE *PALA* OR MULE'S-FOOT FERN (*Marattia Douglasii* (Presl.) Baker) IN THE HAWAIIAN ARCHIPELAGO

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The Hawaiian ferns have constituted an interesting subject of botanical investigation for over a century. There have been few studies, however, of specific ferns or fern groups.[1] The present paper aims to give a concise account of the "mule's-foot" fern or *pala* (*Marattia Douglasii* (Presl.) Baker). This species is of particular interest because it is the sole representative, in the present Hawaiian flora, of an extremely important group of pteridophytes, namely, the Marattiales. Moreover, it also occurs in the Fiji Islands, and this fact raises some interesting questions as to its geographic dissemination. The *pala* was also used as food and medicine by the primitive Hawaiians. Finally, Campbell's[2] studies of the gametophyte stage have given local workers a special interest in this fern.

In early geologic periods Marattiaceous ferns abounded, and comprised an important element in the luxuriant fern jungles of those times. They were very abundant in the Pennsylvanian (Upper Carboniferous), in the Triassic (Rhetic), and in the Mesozoic of India. A survey of the geological record shows that the present-day Marattiales are but scant and skrunken remnants of a magnificent vanished flora.

The ancient and primitive family Marattiaceae is represented

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[1] MacCaughey, V. Genus Gleichenia in the Hawaiian Islands. Torreya **18**: 41–52. 1918.

[2] Campbell, D. H. Observations on the development of *Marattia douglasii* Baker. Ann. Bot. **8**: 1. 1894.

[No. 12, Vol. 18 of Torreya, comprising pp. 231–258, was issued 21 January 1919]

in the Hawaiian flora only by a single species, *M. Douglasii.* The geographic range of the family is indicated by the following table:

Genus	No. of species	Range
Marattia	25	tropics
Angiopteris	1 (or 60!)	Old World tropics, Australasia, S. Japan
Archangiopteris	1	southwestern China
Kaulfussia	1	Indo-Malaya, Philippines
Macroglossum	1	Borneo
Danaea	20	Tropical America

From this table will be seen that Hawaii, isolated in the vast stretches of the North Pacific Ocean, and lying on the rim of the tropics, is the northernmost limit of the family's range in the entire Pacific basin.

Three theories may be presented to explain the occurrence of *M. Douglasii* in the Hawaiian Islands. First: It also occurs in the Fiji Archipelago. Inasmuch as the bulk of the native Hawaiian flora shows affinities with that of the southwest Pacific, it is possible that the *pala* was introduced through natural agencies,—ex. wind,—from the South Pacific. Second: The native Hawaiians habitually used the *pala* for food and medicine. The natives originally migrated to Hawaii from Tahiti, and for many centuries maintained intercourse with their southern kinsfolk. During this period of migration and intercourse, numerous food plants[1] were introduced into Hawaii. It is not at all unlikely that the *pala* was deliberately introduced, by the natives, during this epoch. Its present distribution in the islands is in no way incompatible with this hypothesis.

Third: The entire Hawaiian Archipelago has undergone profound subsidence during recent geologic time.[2] In early times the islands were united by land connections. This formed a "Pan-Hawaii-land," very much larger in area, higher in elevation, and diversified in topography and climate, than the present archipelago. On the warm lowlands of Pan-Hawaii-land may have existed great tropical jungles of Marattiaceous ferns and their allies. All have vanished save the lone *M. Douglasii*, that was able to survive under the changing ecologic environment. There is ample evidence elsewhere in the Hawaiian flora to show that many elements of the present flora are but remnants of the far richer flora of Pan-Hawaii-land.

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[1] MacCaughey, V. Food Plants of the Ancient Hawaiians. Sci. Monthly **4**: 75–80. 1917.

[2] MacCaughey, V. Outstanding Biological Features of the Hawaiian Archipelago. Amer. Nat. in press.

The genus *Marattia* Sm. (—*Dicostegia* Presl., *Eupodium* J. Sm., *Gymnotheca* Presl., *Marattia* Presl., *Myriotheca* Bory, *Stibasia* Presl.) was named in honor of an Italian botanist, J. F. Maratti, of Vallombrosa, Tuscany, who lived in the seventeenth century and wrote on ferns. The genus comprises about 25 species, which are scattered throughout the tropics, and into the southern hemisphere. The following table shows the distribution of the better-known species.

OLD WORLD

African

fraxinea Sm.—west coast of Africa to Polynesia.
salicifolia Schrad.—South Africa to the Cape.
Boivini Mett.—Madagascar.
purpurascens de Vriese—Ascencion Island.

East Indies

salicina Sm.—East Indian Archipelago.
sambucina Bl.—Java.
pellucida Presl.—Philippine Islands.

Melanesia

melanesiaca Kuhn—Melanesia.
attenuata Labill—New Caledonia.

Polynesia

Douglasii (Presl.) Baker—Fiji, Hawaiian Islands.

NEW WORLD

cicutifolia Kaulf.—tropical America.
Kaulfussii J. Sm.—tropical America.
alata Sm.—West Indies, Mexico, northern South America.
Weinmanniifolia Liebm.—Mexico.
laevis Sm.—West Indies.

Marattia Douglasii (Presl.) Baker[1] is called *pala* by the Hawaiians. It may also be called the Mule's-foot Fern, or Douglas's Marattia. It was named in honor of the Scotch botanist, David Douglas, who visited Hawaii in 1833, and lost his life by falling into a native cattle-trap.

It is a large, coarse-leaved, showy fern, easily recognized in the forest. Although not as large as the Marattias of other countries, it attains generous size, with a stocky trunk 1–2 ft. high, and wide-spreading leaves, 6–15 ft. long. In Hawaii Marattia is surpassed in stature and spread by some of the arborescent species (*Cibotium*, *Sadleria*[2]). Aside from the strictly arborescent species, however, *Marattia* and *Angiopteris* may be ranked among the largest of the ferns.

The *pala* is abundant in the mountain-forests of Hawaii, and in the moister parts of the lower forests. It inhabits the humid zone lying between 800–3500 ft., on both windward and leeward slopes. It favorite haunts are cool, heavily shaded, humid, steep-sloped ravines, where it forms little colonies or patches. It seems to prefer sharply sloping banks and ravine-sides, although it is also found in level places. The *pala* is strongly hygrophytic and shade-loving; it is never found in dry or exposed situations.

Representative regions where the *pala* is abundant are: Hanalei and Na Pali districts, Kauai; Kaala and Punaluu districts, Oahu; valleys of northeastern Molokai; mountains back of Lahaina and Wailuku, Maui; forests of windward Haleakala, Maui; forests of Hilo, Hamakua, Olaa, and Kona, Hawaii. There are no places where it is excessively abundant; it is scattered rather sparingly through the forests and groves.

The stem or trunk is tuberous, barrel-shaped, or almost globular. It is stocky and erect, as is also true of *Angiopteris*. *Danæa* and *Kaulfussia* have more or less horizontal rhizomes. The *pala* stem is sometimes half buried under leafmould and earth, but on the steeper slopes, where the *pala* best luxuriates, it is almost wholly exposed.

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[1] W. J. Hooker and J. G. Baker. Synopsis Filicum. London, 1868, p. 441. Also called *Stibasia Douglasii* Presl., *Gymnotheca Douglasii* T. Moore, *M. alata* Hook. & Arn.

[2] MacCaughey, V. Tree Ferns of Hawaii. American Botanist, **22**: 1–9. 1916.

The stem is completely covered by the conspicuous, dark, fleshy auricles (stipules) and leaf-bases. The petioles arise from among the brownish or purplish auricles. After the fall of the leaf the fleshy base remains alive and often gives rise to adventitious buds. Hooker, in describing the stipules of *M. purpurascens* De Vriese states that they may become "leafy at the margin, lobed and crestd, green, sometimes even becoming soriferous pinnules." The leaf-bases of the *pala* have been well described by Camptell:[1]

> "The leaves are furnished at the base with very conspicuous fleshy stipules which remain adhering to the stem after the leaf has fallen away, and these leaf-bases, with their attached stipules, more or less completely cover the surface of the stem. As the leaves fall away they leave a characteristic scar marked by the remains of the vascular bundles. The leaf-base as well as the stalks of the leaflets show a more or less marked enlargement, recalling the pulvinus which occurs so commonly in the Leguminosae. It is at this point that the leaf-stalk separates, the smaller divisions of the leaf often breaking away from the main or secondary rachis, in the same fashion as the main leaf-stalk falls. In the large species of *Marattia* and *Angiopteris* this enlarged leaf-base with the two thick, fleshy stipules curiously resembles in shape and size the hoof of a horse."

The present writer would suggest that the comparison with a mule's hoof would be more apt, and proposes as the common name, "MULE'S-FOOT" FERN.

The thick, fleshy auricles are richly supplied with starch and mucilage, and were used by the primitive Hawaiians as an article of food, when other food supplies were lacking. The "mule's feet" were baked in hot ashes, whereupon they became very palatable. The writer has frequently eaten baked *pala*, and can testify to its excellence. The *pala* stipules were also used medicinally, for bronchial and intestinal catarrh. Slices soaked in cold water soon impart their mucilage to the liquid, and form a pleasant drink.

In cross section the starchy, watery stem shows a complicated system of steles, arranged in concentric circles. Sclerenchyma is absent from its ground tissue.

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[1] D. H. Campbell. The Eusporangiatae, 1911, p. 118.

The *pala* roots are short, thick, and fleshy. They originate with reference to the stele circles in the stem. The central cylinder of the root has several alternating groups of xylem and phloem. Tannin sacs are abundantly developed in the roots, as well as in other parts of the plant.

The *pala* foliage is stately and somber. The leaves are few in number (5–150), spirally arranged, and with close-set bases. The young leaves are enclosed in the prominent stipules; the leaves are circinate, and slowly unfurl in the typical fern manner. The leaves develop very slowly,—a period of 3 to 6 months being required for the unfurling of a single leaf. Indeed, all of the vital functions of the *pala*, like those of other rain forest plants, are very sluggish.

The petioles are 3 to 5 feet long, stout, smooth, and shining. At the base they are conspicuously swollen, articulate, and 2.5–3 ins. in diameter. The "mule's-foot" base, with its two large, fleshy, auricular stipules, has already been described. Lenticel-like structures are of common occurrence on the older leaf-bases. They arise beneath the stomata, and form small cavities, the peripheral cells of which become detached and dried up. Large mucilage ducts and numerous tannin sacs are developed in the petioles of the older leaves.

The leaf-blade is 3 to 8 ft. long, deltoid or ovate-oblong, and 2–3-pinnate. The base is 3-pinnate; there is a terminal pinnule. The blade is a characteristic dark green, smooth, glossy, and notably fleshy. The color and texture are quite distinctive. A cross-section of leaf reveals a thick layer of collenchymous hypodermal tissue.

The pinnae are oblong-lanceolate. The lowest pinnae are 6–24 in. long, on stalks of .5–2.5 in. The upper portion of the rachis is narrowly margined or winged. The secondary pinnae are linear, 3–6 in. long, with a broadly compressed or winged rachis. The ultimate pinnules are substipitate, ovate or oblong, .5–1 ins. long by .25–.30 in. wide, and bluntly serrate. The apex is obtuse or acuminate; the base is cuneate or subtruncate. The veins are simple or dichotomously forked.

All the leaves are spore-bearing or potentially so. The sporangia are large, fleshy, and borne in boat-shaped groups (synangia), on the under surface of the pinnule, near the margin. The sporangia, each of which arises from a number of superficial cells, are incompletely separated from one another, and remain together in the oblong or capsule-like synangia. The walls of the sporangium are several cells in thickness. The annulus is wanting or greatly reduced; there is no indusium. The synangium is adnate to the vein, or very short-stalked. Dehiscence is first by the opening of the synangial valve, then slits along each sporangium.

Campbell[1] has made detailed studies of the gametophyte. The spores are very small, bilateral or tetrahedral, and yellowish-brown. Under suitable conditions they germinate promptly. Within a week they begin to show a greenish tint, due to the developing chlorophyll. The mature gametophyte is large, fleshy, massive, dark-green, and heart-shaped. It grows on the surface of the soil and closely resembles such liverworts as *Pellia*. It is broad heart-shaped, tapering to a narrow base. The very old gametophytes branch dichotomously exactly as in the thallose liverworts. "A broad midrib extends for nearly the whole length of the thallus and merges gradually into the wings, which are also several-layered, nearly or quite to the margin"—Campbell. Rhizoids,—brown, unicellular, and thin-walled,—are produced abundantly from the cells of the lower surface.

The gametophyte is monoecious. Antheridia appear first, sometimes on the upper surface, but usually along the lower side of the midrib. The archegonia are confined exclusively to the lower surface of the midrib. Campbell points out that the reproductive organs are very much like those of *Ophioglossum*, and are "marked indications of the primitive nature of these ancient ferns."

The *Marattia* gametophyte is always infested with a specific endophytic fungus. Campbell states that it is probably identical with or very closely related to the fungus which occurs in *Ophioglossum*. "In the infested cells of the green gametophyte the starch and chromatophores are destroyed by the action of the endophyte, but the nucleus of the cell remains intact." The duration of the gametophyte is apparently unlimited, so long as fertilization does not take place. The young sporophyte consists at first mainly of the primary leaf and root, which are traversed by a single axial vascular strand. A stem apex is developed at an early period, although it remains relatively inconspicuous.

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[1] D. H. Campbell. The Eusporangiatae, 1911. Mosses and Ferns, 1905.

The *pala* does not occur in cultivation, to the writer's knowledge. It undoubtedly would grow successfully under humid fern-house conditions, as do many other Hawaiian ferns. *M. fraxinea* Smith, which ranges from west Africa to New Zealand, is cultivated in American conservatories. The Hawaiian *pala* would likewise give a magnificent tropical effect in northern greenhouses. It deserves attention.

PLEISTOCENE PLANTS FROM TENNESSEE AND MISSISSIPPI

By Edward W. Berry

I have published, from time to time, brief accounts of Pleistocene plants from our Atlantic and Gulf states as they have passed through my hands, since the amount of material likely to be available does not warrant a more comprehensive treatment. For this reason I wish to place on record the following new occurrences.

It is to be hoped that the distribution of our floras in the era immediately preceding the present be considered by botanists dealing with the existing flora. Even in the present unsatisfactory state of our knowledge of Pleistocene plants, woefully behind that of other civilized countries, much is to be gained in insight and many pitfalls may be avoided by looking back of the present.

This note relates to small collections made by Bruce Wade in 1915 at Adamsville, McNairy County, Tennessee, from next to the highest terrace of the Tennessee River (elevation about 500 ft.), and by E. W. Shaw from the Loess just west of